

Colonization of Marine Fishes in a Newly Created Harbor, Honokohau, Hawaii¹

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ABSTRACT: This study follows the colonization of marine fishes in a newly created Hawaiian harbor over a 5-year period. The inner harbor serves as a nursery ground; habitats in this area are distinguished by high turbidity, lowered salinities, long water-residence times, and a general lack of cover that renders the area unsuitable for colonization by many coral reef fishes. There appears to be a diminishing gradient of these characteristics in a seaward direction, which may be causal to the observed increase in marine fish species.

A simple colonization curve (number of species over time) suggests that 80–87 species represented an equilibril number of species under ecological conditions as they existed at the termination of this study within the harbor; about 50 months following construction was required to attain this status. The data suggest that seven of these colonizing species appear to be the most opportunistic. These fishes are probably generalists in their habitat requirements, and thus may be expected to colonize and persist in other similar newly opened habitats in the Hawaiian Islands.

A NUMBER OF STUDIES have concerned themselves with the colonization of inshore fishes on coral reefs. Randall (1963) followed the colonization of fishes on a concrete block reef in the Caribbean, and Wass (1967) defaunated a patch reef in Kaneohe Bay, Hawaii, and studied subsequent recolonization. Sale (1974, 1975, 1977, 1978), Russell, Talbot, and Domm (1974), and Sale and Dybdahl (1975), working on the Great Barrier Reef, obtained evidence leading to the hypothesis that chance factors were responsible in determining the outcome of colonization. Using small artificial patch reefs, Talbot, Russell, and Anderson (1978) found no persistent species equilibrium in the colonizing fish communities. Their data suggest that reef fish communities do not attain an or-

dered state. Work in the Caribbean (Smith and Tyler 1972, 1973) alluded to resource-sharing adaptations that may allow a greater species packing as well as determine which species are found together in a given community (C. L. Smith 1977, 1978). This deterministic viewpoint has been furthered by research conducted on recolonizing fish communities in the Gulf of California (Thomson and Lehner 1976, Molles 1978) and in the Gulf of Mexico (G. B. Smith 1979). Interestingly, a number of investigators (Russell et al. 1974, Nolan 1975, Molles 1978, Talbot et al. 1978) have found little or no obvious correlation between reef substratum complexity (or habitat heterogeneity) and the species diversity of colonizing fishes. In Hawaii, Brock, Lewis, and Wass (1979) determined that recolonizing fish communities were relatively predictable in their species composition. The latter authors concluded that the study of fish colonization in small areas lends support to the chance factor hypothesis and a nonequilibrium state; however, if the investigation encompasses a large area relative to home ranges of most species, the colonization pro-

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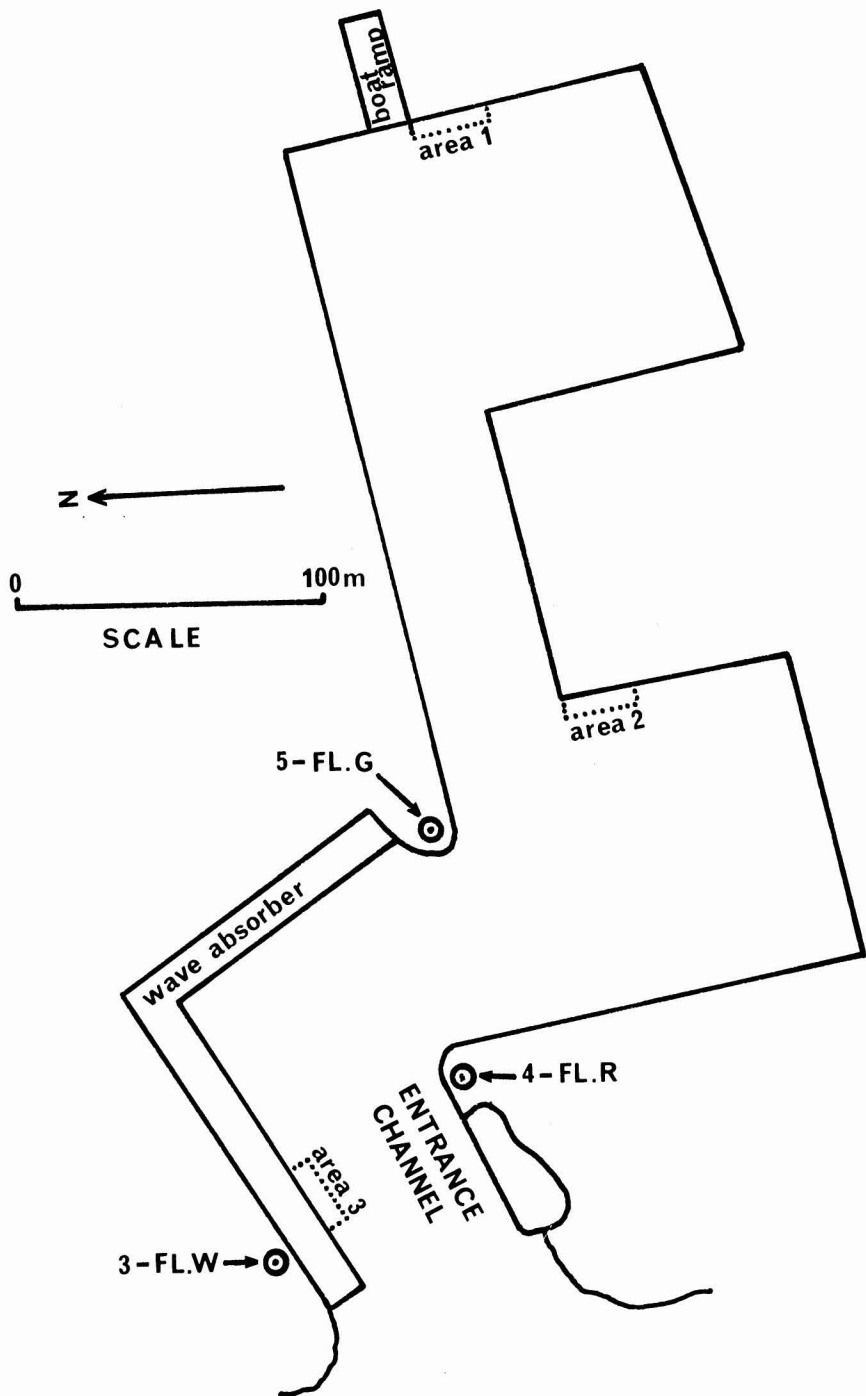


FIGURE 1. Outline map of Honokohau Harbor, Hawaii, showing the approximate locations of the first three study sites.

cess is deterministic, leading to a predictable community structure.

The growth and maintenance of coral reef fish communities is probably partially dependent on the physical stability of the environment. If a habitat available for colonization is suboptimal due to adverse physical conditions, how will colonization by marine fishes proceed? Will the species composition of the resultant community be stable? The present research conducted in a newly created harbor over a 5-year period attempts to answer these questions.

MATERIALS AND METHODS

Honokohau Small Boat Harbor located on the Kona, Hawaii, coast was quarried from a *pahoehoe* lava flow and completed in March 1970, thus representing a newly created habitat for fish colonization. This study has been conducted as an annual survey in its first 3 years—the first phase in October 1971, the second in September 1972, the third in August 1973—and a final assessment was made in August 1976. Three sites within the harbor have been sampled (Figure 1). During each survey the assemblage of fishes within the harbor are compared to a community existing outside the harbor in an undisturbed area.

To assess changes in the fish populations of the harbor, visual census methods (Brock 1954) were used; that is, a diver carrying a slate (inscribed with the names of most fish species encountered) slowly swam along a previously set transect line and tallied the numbers of each species seen within a predetermined area. All underwater observations were made using SCUBA equipment.

All transects were 25 m in length. At study area 1 (Figure 1) fishes found along the wall and in the water column from the surface out to where the bottom levels off (2.5 m deep) were censused. The substratum consists of a steep slope (45°) of basalt fragments grading into thick silt on the adjoining level bottom. Turbidity in this area is high, resulting in poor visibility (maximum =

3.5 m), and a 0.75–1.0-m-thick lens of cool low-salinity water overlies the warmer seawater. In study area 2, enumeration of fishes was undertaken from the surface down the slope of the harbor wall to a point where the bottom levels off. The substratum of this site consists of a nearly vertical basalt wall (3.5 m high underwater) with some lava rubble at the base. The adjoining flat bottom is covered with silt and sand. The surface lens of low-salinity water occurs in this area to a depth of 0.75 m, and turbidity is less than in area 1, with a resulting visibility of about 5–6 m. Study area 3 is located along the breakwater on the northern side of the entrance channel. The substratum consists of large boulders, affording a maximum cover down to a 5-m depth, where it levels off to a sand and silt bottom. Fishes were counted from the surface down to a 30° slope to the point of level bottom. Of the three study sites, this area is the most exposed to normal marine conditions, resulting in less turbidity (visibility to 12 m) and a lessening of the influence of the mixohaline lens (thickness to 0.50 m).

During each of the surveys, a census of fishes residing outside the harbor was carried out. The locations of these transects (area 4) were random, but they were chosen such that substratum and depths were similar. The depths at which these transects were performed are as follows: 1971, 6.5 m; 1972, 10.5 m; 1973, 8–11 m; and 1976, 10 m. All area 4 transects were conducted on a substratum of basalt and live coral and are probably representative of undisturbed habitats at those depths along this portion of the Kona coast. The object of the data taken in area 4 is to serve as a relative comparison of the communities of fishes found within the harbor to the assemblage found outside in an undisturbed habitat. A 25-m line was laid, and following a 15-min wait away from the transect line (to reduce the fright in some fishes caused by the presence of a diver) a census of all fishes within a 6 × 25-m corridor (to the water surface) was made.

In conjunction with the censuses taken in the above four study areas during the 1972, 1973, and 1976 surveys, a checklist of all

species of fishes seen within the harbor was prepared. This was accomplished by a diver with SCUBA equipment swimming along all the walls within the harbor seaward as far as the two harbor lights (Figure 1) and noting all fish species seen.

Inside the harbor two censuses were made during every survey at each of the three study areas. The first census was taken near the peak of the rising tide and the second was taken 4–6 hr later, near the lowest part of the falling tide. Time permitted only one census of the fishes on the transect outside the harbor and only one swim around the harbor walls in making up the checklist of species.

The method of visual censusing is subject to several observer errors, some of which have been discussed by Brock (1954), Wass (1967), Jones and Chase (1975), Jones and Thompson (1978), and Russell et al. (1978). Secretive species are usually underestimated, e.g., the moray eels (family Muraenidae) and squirrelfishes (family Holocentridae). Another source of error is failure to see cautious species, which may leave the area of the transect before the counting has begun. This frightening of some species by the presence of a diver may be diminished by reducing the amount of time spent in the water in the area of the transect just prior to the actual census. To decrease time in the water before sampling, the 25-m transect lines were laid in study areas 1, 2, and 3 some 15–18 hr before the first census took place during the 1972, 1973, and 1976 surveys. The effectiveness of the visual method is reduced in turbid water, and species that move quickly and/or are very numerous make accurate counts difficult. In spite of these drawbacks, the visual census method is still useful in comparing relative abundance of diurnally active fishes in the four study areas.

RESULTS

The results of the fish censuses by station, year, and species encountered are given in Appendix A. It is apparent that there has

been an increase in fish species and individuals with time in the harbor.

Due to differences in the amount of substratum relief present in each of the four study areas, it is impossible to equate surface areas. Therefore any comparisons of the absolute numbers of individuals between areas is not justified. Relief provides a structural heterogeneity to the habitat; it increases shelter, nesting, and feeding sites for reef fishes, and thus may be an important agent in governing the number of individuals and species within any one study area.

One hundred twenty-one fish species have been seen within the harbor over the 5-year study period. Thirty-two species have been present during every survey; since 1972 there have been 41 species and since 1973 there have been 57 species. These data are drawn from the checklist of species (Appendix A) in which only one individual of a species may have been sighted. Few species were encountered in any study area during every survey; those species that were are presented in Table 1. Eight species were present every year at the innermost harbor station, 14 species in the midharbor station, and 20 species at the outer harbor site. Fish species present in abundance every year on the transects and throughout the harbor include *Acanthurus nigrofuscus*, *A. triostegus sandvicensis*, *Ctenochaetus strigosus*, *Aulostomus chinensis*, *Mulloidichthys flavolineatus*, *Parupeneus multifasciatus*, and *Abudefduf abdominalis*. In this assemblage are three herbivores, three carnivores, and one planktivore. *Acanthurus nigrofuscus* and *A. triostegus sandvicensis* browse on filamentous algae, but *Ctenochaetus strigosus* is a grazer on diatoms and detritus (Jones 1968). Randall (1967) notes that *Aulostomus chinensis* feeds on small fishes and caridean shrimps. *Mulloidichthys flavolineatus* feeds on sand-dwelling invertebrates, and *Parupeneus multifasciatus* feeds on benthic crustaceans (Hobson 1974). *Abudefduf abdominalis* is a planktivore that feeds on copepods in Kona, Hawaii, waters (Hobson 1974). Some of these fishes are generalists in their feeding habits; for example, *Abudefduf abdominalis*

TABLE 1
FISH SPECIES ENCOUNTERED IN CENSUSES EVERY
YEAR FOR EACH STATION WITHIN HONOKOHAU
HARBOR (× INDICATES THE PRESENCE OF THE SPECIES
AT THE STATION)

SPECIES	STATION		
	1	2	3
<i>Acanthurus achilles</i>			×
<i>A. nigrofuscus</i>	×	×	×
<i>A. nigroris</i>		×	×
<i>A. triostegus sandvicensis</i>	×	×	×
<i>Ctenochaetus strigosus</i>	×	×	×
<i>Zebрасoma flavescens</i>			×
<i>Apogon maculiferus</i>	×	×	
<i>Aulostomus chinensis</i>	×	×	×
<i>Canthigaster jactator</i>			×
<i>Chaetodon lunula</i>		×	
<i>C. miliaris</i>			×
<i>Forcipiger flavissimus</i>			×
<i>Stethojulis balteata</i>		×	×
<i>Gomphosus varius</i>			×
<i>Thalassoma duperryi</i>		×	×
<i>T. purpuraceum</i>			×
<i>Mulloidichthys flavolineatus</i>	×	×	×
<i>Parupeneus multifasciatus</i>	×	×	×
<i>P. porphyreus</i>		×	
<i>Ostracion meleagris</i>		×	×
<i>Abudefduf abdominalis</i>	×	×	×
<i>Stegastes fasciolatus</i>			×
<i>Scarus</i> spp. (juveniles)			×
Total number of species	8	14	20

in Kaneohe Bay, Oahu, feeds heavily on polychaete larvae.

DISCUSSION

As the gradient of physiological stress increases in an environment, the number of species present diminishes continuously along this stress gradient (Sanders 1969). The innermost portions of Honokohau Harbor (area 1) are most probably subjected to greater physical fluctuations (i.e., salinity, water clarity) than the outer stations (areas 2 and 3). Area 1 probably has the longest water-residence time of the three study sites. It is the shallowest, and the depth of the mixohaline water layer is greatest in area 1 and decreases moving seaward. Human dis-

turbance probably also has its greatest impact in area 1. Since the 1973 survey there has been an increase in use of Honokohau Harbor; disturbance to marine communities in the vicinity of area 1 is greater today than previously, with the building of a fuel dock along the shoreline of station 1. Study area 4 lies outside these influences. The greater disturbance present at station 1 is reflected in the fewer species encountered at this site.

The fish community at station 1 (inner harbor) is apparently comprised of juveniles. The majority of fishes met with in study areas 2 and 3 appear to be adults or subadults; however, some juveniles of *Acanthurus triostegus sandvicensis*, *Kuhlia sandvicensis*, *Thalassoma duperryi*, *Mulloidichthys flavolineatus*, *M. vanicolensis*, *Abudefduf abdominalis*, *Apogon maculiferus*, and *Scarus* spp. were censused. Over the period of this study, recruitment to areas 2 and 3 has been principally by adults and subadults and by juveniles in study area 1. The preponderance of juveniles in area 1 during this time suggests that this area may be serving as a nursery ground. Wass (1967) and Brock et al. (1979) found that recruitment to a poisoned patch reef in Kaneohe Bay, Hawaii, was primarily by adults or subadults. However, a number of other studies, e.g., in the Caribbean (Randall 1963), the Red Sea (Gundermann and Popper 1975), Australia (Russell et al. 1974, Sale and Dybdahl 1975, Talbot et al. 1978), and at Enewetak Atoll (Bussing 1972, Nolan 1975), have noted juveniles to be the major source of recruitment to artificial and previously defaunated reefs.

Bottom relief is probably an important parameter in the distribution, community composition, and number of fishes found in an area. The greatest amount of relief on all surveys and transects was in area 4. Area 3 was next in the amount of relief present, followed by area 1 and, lastly, area 2. This is suggested by a comparison of the total number of individual fishes present in each study area (Appendix A). It should be noted that the discrepancy in the number of species and individual fishes between surveys at

APPENDIX A

FISHES OBSERVED AND CENSUSED IN EACH OF THE FOUR STUDY AREAS FOR EACH OF THE FOUR SURVEYS

FAMILY AND SPECIES	1971					1972					1973					1976				
	1	2	3	4	CL	1	2	3	4	CL	1	2	3	4	CL	1	2	3	4	CL
Acanthuridae																				
<i>Acanthurus achilles</i>			5	2	×			5		×			1		×			3		×
<i>A. dussumieri</i>					×	1	2	2	7	×	2	10		2	×	8	6	2		×
<i>A. glaucopareius</i>				4																
<i>A. guttatus</i>													4		×			6		×
<i>A. leucopareius</i>			2	1	×			7		×								3		×
<i>A. nigrofuscus</i>	2	3	28	20	×	6	8	29	21	×	4	10	37	42	×	33	32	82	95	×
<i>A. nigroris</i>		4	2	2	×	3	2	9	19	×	1	1	5	12	×	2	4	6	3	×
<i>A. olivaceus</i>		1		4	×	1	15	12	32	×	1	19	1	1	×	4	10	1	6	×
<i>A. thompsoni</i>									3				1		×					
<i>A. triostegus sandvicensis</i>	50	19	26	3	×	52	26	21	10	×	12	17	15	10	×	46	45	116	18	×
<i>A. xanthopterus</i>		2			×							2		8	×	9	7	2		×
<i>Ctenochaetus strigosus</i>	15	12	11	29	×	25	45	31	93	×	20	46	50	68	×	13	34	57	126	×
<i>C. hawaiiensis</i>																	2		6	×
<i>Naso brevirostris</i>														1						
<i>N. literatus</i>				2	×	1		2	14	×		2			×	3	2		2	×
<i>N. unicornis</i>				2		1	2	1		×	1				2					
<i>Naso spp. (juveniles)</i>	1	2			×															
<i>Zebrasoma flavescens</i>			2	9	×			1	9	×			4	69	×		25	18	88	×
Apogonidae																				
<i>Apogon maculiferus</i>	1	12			×	19	14	2	2	×	1	2			×	42	100	11		×
<i>A. menesemus</i>											1				×					
<i>A. snyderi</i>						1	3		3	×	4	19	2	6	×		19	11	6	×
<i>Foa brachygramma</i>											9	1			×	7	1			×
Aulostomidae																				
<i>Aulostomus chinensis</i>	10	2	4	3	×	3	2	3	2	×	2	2	5		×	3	6	5	4	×
Balistidae																				
<i>Melichthys niger</i>									1						1				1	
<i>M. vidua</i>																	1		2	×
<i>Rhinecanthus aculeatus</i>				4	×															
<i>R. rectangulus</i>																			1	
<i>Sufflamen bursa</i>									4						7					
<i>S. frenatus</i>									3						3				3	
Blennidae																				
<i>Cirrhipectus</i> sp.																				×
<i>Runula goslinei</i>			1	1	×			1	1	×							2		4	×
Bothidae																				

[illegible]

APPENDIX A

[illegible]

[illegible]

APPENDIX A (cont.)

FAMILY AND SPECIES	1971					1972					1973					1976				
	1	2	3	4	CL	1	2	3	4	CL	1	2	3	4	CL	1	2	3	4	CL
Priacanthidae								1		×				1						
<i>Priacanthus cruentatus</i>																				
Scaridae								1	1	×				4	×		1			×
<i>Calotomus</i> sp.							1		1	×				3			1		3	×
<i>Scarus dubius</i>							1	1	1	×			1	7	×			2	4	×
<i>S. perspicillatus</i>														5	×		1		13	×
<i>S. sordidus</i>	2				×				4											
<i>Scarus</i> spp. (juveniles)			2	4	×	23	8	7	17	×	1	15	12		×	2	31	11		×
Scorpaenidae																				
<i>Dendrochirus brachypterus</i>		1			×						1	1			×	1	1			×
<i>Pterois sphex</i>									1					9					9	
<i>Scorpaena coniota</i>								1		×			1		×					
<i>Taenianotus triacanthus</i>																				
Serranidae																				
<i>Cephalopholis argus</i>										×				1						
Sparidae									12					12						
<i>Monotaxis grandoculis</i>																				
Synodontidae					×		1	3	1	×		1		1	×	1	1	2	1	×
<i>Saurida gracilis</i>															×	1				×
<i>Synodus dermatogenys</i>																				
Tetradontidae																				×
<i>Arothron hispidus</i>																				
<i>A. meleagris</i>					×					×										
Zanclidae					×		1	1	1	×		2	3	2	3	×	1	1	1	×
<i>Zanclus cornutus</i>																				
Total number of species	18	22	28	37	54	33	38	46	69	68	25	37	40	73	72	34	52	54	61	90
Total number of individuals	115	93	225	210		245	244	381	689		142	337	310	728		325	592	629	845	

NOTE: The numerical values given under areas 1, 2, and 3 for each year are the average of two censuses; those under the area 4 columns are for a single census. The checklist of all species seen within Honokohau Harbor is given in column 5 under each year (marked CL). Most species' names are those of Gosline and Brock (1960).

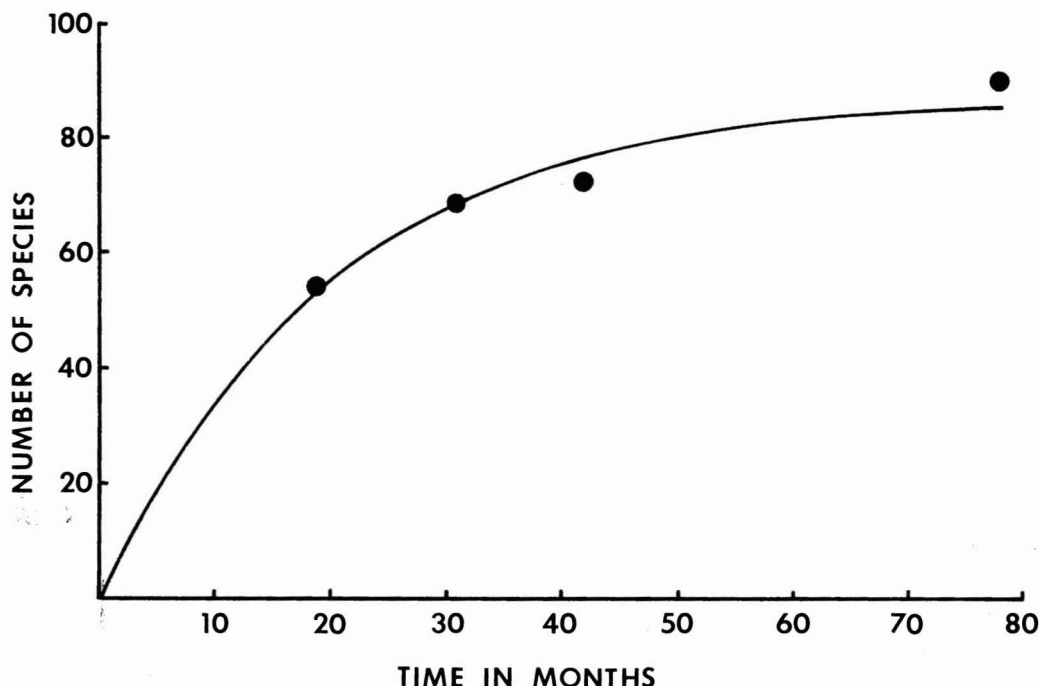


FIGURE 2. Plot of the total number of fish species colonizing Honokohau Harbor. Species equilibrium is approached after 50 months at about 80 species; data drawn from the checklist of species in Appendix A.

station 4 is probably due to the choice of area sampled. A slight change in the bottom type and topography over a short linear distance (2–5 m) may be reflected in large differences in the species and number of fishes encountered.

Considering the harbor as a vacant habitat being colonized by fishes, one measure of colonization is the number of species present within the harbor at the time of census. Such presence or absence data may provide evidence of an equilibrium phenomenon albeit the fact that recruitment to the harbor is by simple invasion from adjacent communities. If the vacant habitat is of sufficient size (or is isolated), the number of species accumulating after a period of time will attain and remain at a near constant level, thus demonstrating an equilibrium (Simberloff 1976). A colonization curve (the number of species present plotted against time, as presented in Figure 2) may be described by a simple asymptotic growth function for the fish species colonizing Honokohau Harbor:

$$\hat{y} = 87.52(1 - e^{-0.049t})$$

where \hat{y} is the expected number of species present at time t (in months). This equation provides an excellent fit to the data ($R^2 = 0.99$). The colonization curve only quantifies the total number of accumulated species and does not measure the persistence of any colonizing species.

Experimental studies by Cairns et al. (1969), Simberloff and Wilson (1969, 1970), Wilson and Simberloff (1969), Maguire (1971), Schoener (1974a, 1974b), Simberloff (1976), Schoener, Long, and DePalma (1978), and Brock et al. (1979) suggest that an equilibrium number of species may be approached during colonization; this is usually based on the decreasing slope of the convex colonization curve (i.e., approaching an asymptote). Such a curve may be expected to oscillate about the equilibrial number of species (Maguire 1971, Schoener 1974a), but an asymptotic function suggests a degree of stability in the colonizing fish communities. In the present study, the col-

onization curve of fishes recruiting to Honokohau Harbor levels off after 50 months; this translates to an approximate equilibrium number of 80 fish species (Figure 2). The harbor is not a totally isolated entity to marine fishes. There are a number of wandering species that probably comprise a small proportion of the total fish assemblage found within the harbor. The walls of Honokohau Harbor represent a large sampling area used in making up the checklist of species which provides the data for the colonization curve (Figure 2). With such a large sampling area, many wandering and rare species will be met with, leading to their inclusion during most censuses. Their presence or absence has not appeared to affect the fit of the data to an expected asymptotic colonization curve.

In another study of the colonization patterns of Hawaiian reef fishes, Brock et al. (1979) note that it took more than 21 months for 78 species (the approximate equilibrium number) to colonize a 1500 m² patch reef. These authors found a reasonable level of species persistence (about 40 percent) among the colonizing fishes. In the present study, the number of species that persisted at a station ranged from 24 to 71 percent of the species comprising the community.

The species pool of marine fishes available for colonization to Honokohau Harbor is sizable. In 600 m² of substratum censused for fishes adjacent to the harbor (area 4, Appendix A), 105 species were encountered. The observed assemblage of fishes present in the harbor are those species that are able to find suitable habitats there. As more invertebrates and algal species settle and become established within the harbor, the benthic habitat available to fishes becomes more diverse. Thus, the number of fish species is expected to increase gradually over time to a point of saturation.

The colonization of Honokohau Harbor by fishes is probably not directly regulated by the dispersal ability of the propagules as found in many other studies, because most colonization has been by adults and subadults that commonly occur just outside the harbor. The most important factor regulating the species composition of fishes within

Honokohau Harbor has probably been meeting the ecological requirements of the colonizing species. Honokohau Harbor appears to be a suboptimal environment for many reef fishes. These suboptimal conditions have depressed the asymptote of the colonization curve and favored a certain assemblage of species that are opportunistic generalists in their habitat requirements. Apparently, the most successful species are *Acanthurus nigrofusus*, *A. triostegus sandvicensis*, *Ctenochaetus strigosus*, *Aulostomus chinensis*, *Mulloidichthys flavolineatus*, *Parupeneus multifasciatus*, and *Abudefduf abdominalis*. Four of these species (*Acanthurus triostegus sandvicensis*, *Ctenochaetus strigosus*, *Mulloidichthys flavolineatus* and *Abudefduf abdominalis*) are early and persistent colonists on other Hawaiian reefs (Brock, Lewis, and Wass 1979). These seven species are probably generalists and may be expected to colonize and persist in similar newly opened suboptimal habitats elsewhere in the Hawaiian Islands.

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